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1 TITLE: The difference between night and day: the nocturnal and diurnal activity  
2 budget of gray seals (*Halichoerus grypus*) during the breeding season  
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All pinniped species are constrained to give birth and raise their pups on land or ice (Bartholomew 1970). This constraint has allowed for detailed behavioral observations on several species of pinniped during the breeding season (*e.g.*, Redman *et al.* 2001; Dobson and Jouventin 2003; Maniscalco *et al.* 2006; Young and Gerber 2008). From these observations, activity budgets (also referred to as time budgets) can be calculated; typically to provide information on how individuals, or groups of individuals, partition their time across defined behavioral categories (*e.g.*, Boness 1984; Anderson and Harwood 1985; Arnold and Trillmich 1985; Trillmich 1986; Lydersen *et al.* 1994; Twiss and Franklin 2010). However, observational studies are usually constrained to daylight periods and, as a result, there is little information from behavioral observations on any pinniped species during the breeding season (or whilst hauled-out) at nighttime (gray seals (*Halichoerus grypus*), Anderson 1978, southern elephant seals (*Mirounga leonina*), Galimberti *et al.* unpublished data cited in Galimberti *et al.* 2002). Yet, for some species, such as the gray seal, which breed in temperate regions during autumn and winter, daylight periods can be as little as one third of the circadian cycle.

The paucity of studies investigating nighttime activity budgets of pinnipeds on land (breeding colonies or haul-out sites) has previously been attributed to technological limitations in commercially available night-vision equipment (Shipley and Strecker 1986, Acevedo-Gutiérrez and Cendejas-Zarelli 2011). Where recent technological advances in telemetry devices, for example, have given ecologically important insights into the circadian behavior of pinnipeds at sea (*e.g.*, Jessopp *et al.* 2013) and on their haul-out patterns (*e.g.*, Cronin *et al.* 2009), there still remains only one study to date that has successfully undertaken behavioral observations of a

pinniped species on land during the nighttime (Anderson 1978). In the  
aforementioned study, Anderson (1978) investigated the variation in the daytime and  
nighttime activity budget of one male gray seal during two consecutive breeding  
seasons and found the ‘Look’ behavior, defined as “head up or turned, gaze directed”,  
occurred significantly more during the daytime. Subsequently, a plethora of studies on  
gray seals have used Anderson’s, arguably limited, study to justify using daytime  
observations as representative of the entire 24 h cycle of activity, either explicitly or  
implicitly (*e.g.*, Amos *et al.* 1993; Worthington Wilmer *et al.* 1999; Redman *et al.*  
2001; Twiss and Franklin 2010). This has potentially far-reaching implications on  
studies of energetics, maternal investment and mating behavior, for example, which  
do not consider the possibility of variation in circadian behavior. If a significant  
difference between daytime and nighttime activity budgets exist, then such studies  
may need to re-interpret their findings.

Given the progressive technological advances in night-vision devices, the  
present preliminary study uses commercially available equipment to investigate the  
circadian activity budget of gray seals whilst on the breeding colony. As gray seals  
are capital breeders (Bartholomew 1970), we hypothesize that nighttime (*i.e.*, an  
extended period of darkness) gives individuals’ an important opportunity to increase  
time spent resting and thus limit energy expenditure. The study site was at Donna  
Nook on the North Lincolnshire coast, eastern England, U.K. (53.47°N, 0.15°E),  
which is a National Nature Reserve (NNR) that consists of approximately 1,150  
hectares of salt marsh, sand dune systems and large inter-tidal sand and mud flats.  
During November and December the NNR is host to a large breeding colony of gray  
seals that gathers on the sand flats far inshore close to publicly accessible areas. The

seals also use adjacent areas where public access is restricted; therefore, seals within this region of the Donna Nook breeding colony are not exposed to the high levels of tourists experienced elsewhere within the NNR. It was within the restricted area that the preliminary study took place.

Gray seals are polygynous, colonial, and annual breeders with a discrete, predictable reproductive season (Boyd *et al.* 1962). In the U.K., adult female gray seals come ashore in the autumn, each giving birth to one pup. Movement of postpartum females on the colony is over short distances, and they tend to remain close to their pupping site, rarely moving further than 10 m from their pup (Redman *et al.* 2001). Once females have given birth they become aggressive towards one another (Bonner 1981). Consequently, mothers tend to maintain a minimum distance of 2.5 m from their nearest female neighbor (median distance = 4.36 m, Pomeroy *et al.* 1994). A female will spend 18 d, on average, nursing her pup (Bonner 1972) and on approximately day 16 of lactation she will enter estrus (Pomeroy *et al.* 1999), during which time she will mate with one or more males before returning to sea (Twiss *et al.* 2006). As such, movement on the colony is relatively infrequent and is typically over short distances, which makes this an ideal study system for obtaining data on circadian activity budgets.

The nighttime video footage was recorded using a custom-made weatherproof camera constructed by Astra Communications Ltd (<http://www.astrasec.com/>). The specifications of the camera were: 540TV color/monochrome, 9-22 mm auto-iris lens with a minimum illumination of 0 Lux. A weatherproof Infrared lamp was also used to increase the area of illumination, the lamp had an output of 850 nanometers IR with

a range of up to 40 m and an IR spread of 30°. The camera and the lamp were powered using two 12v batteries and the footage was recorded on to a 32GB SD memory card. The size of the area under observation was limited to approximately 10 m x 8 m by the field-of-view of the camera and the area illuminated by the infrared lighting. Given this limitation, coupled with the fact that breeding adult male gray seals show a considerably greater degree of mobility over the colony than females and pups (Twiss *et al.* 1994), the present study investigated the variation between daytime and nighttime behavior of postpartum females and their pups, only.

In-field behavioral observations were collected using a five min scan sampling approach (Altmann 1974) between 0800-1600 during the 26 November; 7, 8, and 9 December 2010. Observations were conducted at the periphery of the breeding colony from the cabin of a 4x4 vehicle that was parked approximately 10 m from a fence that prevented the seals coming further ashore. The video footage was collected between 1600-0800 over three nights: 25 November and 7 and 8 December 2010. Video footage was played back in real-time and the same sampling approach was used (five min scan sampling). To avoid observer bias all data were collected by a single observer. For each of the days in which observations were undertaken, to allow for the transition between nighttime and daytime, data 30 min either side of morning and evening civil twilight was omitted; these times were taken at Grimsby, U.K. (approximately 10 km north of Donna Nook; <http://www.sunrisesunset.com>).

Using photo-identification, the unique pelage of the females' allowed for identification of individuals (Hiby and Lovell 1990) during the daytime observations and from the nighttime video footage. Where individuals were further from the

camera ( $> 8$  m), it was not always possible to observe the pelage in the video footage during nighttime; in these instances individuals were identified in the video footage prior to the onset of darkness. Individual pups were identified where possible by their association with their mothers. The ethogram comprised of nine behavioral categories for females and four for pups (Table 1). With the exception of social interactions and energy transfer behaviors associated with the mother, the active behaviors of gray seal pups are often ambiguous to interpret. For this reason these behaviors were grouped into the ‘Active’ behavioral category.

Behavioral data for both daytime and nighttime were obtained for five postpartum females and three pups. The other two pups had too few scan samples at night ( $n \leq 20$ ) (typically due to mothers obstructing the field-of-view of the camera); therefore they were excluded from the analysis. The number of daytime scan samples per individual ranged between 98 – 279 for females, and 98 – 276 for pups. Nighttime observations yielded 68 – 276 and 132 – 324 for females and pups, respectively. If an individual was recorded as out-of-sight during daytime or nighttime observations or out-of-frame during nighttime observations, then these data were not included in the calculation for the activity budgets. As expected, based on previous studies (Anderson and Harwood 1985, Kovacs 1987), the gross activity budget showed that both females (Fig. 1) and pups (Fig. 2) spent the vast majority of their time resting.

To control for repeated observations on the same individuals and to avoid pseudoreplication we employed binomial Generalized Estimating Equations (GEEs) (Hardin and Hilbe 2013) using the *geepack* package (Højsgaard *et al.* 2006) in R (R Core Team 2013). The difference between resting during daytime and nighttime was

150 compared for females and pups separately. The response variable was whether or not  
151 the individual was recorded as resting during each five min scan sample. As residual  
152 autocorrelation was an issue, an auto-regressive (AR1) correlation structure was  
153 included in the GEEs (Hardin and Hilbe 2013). The sole explanatory variable,  
154 whether the observation took place during daytime or nighttime, was included as a  
155 factor.

156  
157 For females and pups the time of day was highly significant, with both females ( $P$   
158  $<0.001$ , Estimate = 0.635, SE = 0.048, Wald  $\chi^2= 173.9$ ) and pups ( $P <0.001$ , Estimate  
159 = 0.756, SE = 0.133, Wald  $\chi^2= 32.5$ ) resting more during the nighttime. As females  
160 have finite energy reserves and a discrete and limited time period to maximize energy  
161 transfer to the pup to enhance pup survival (Hall *et al.* 2001), the significant increase  
162 in the time spent resting at nighttime, for both female and pup, could be an example of  
163 adaptive behavioral plasticity, where both mother and pup are maximizing the  
164 opportunity to conserve energy. Furthermore, the females' activity budget suggested  
165 that vigilance behavior decreased during nighttime, which is similar to Anderson's  
166 (1978) findings for male gray seals. As discussed by Anderson (1978), this makes  
167 biological sense, as in-air visual acuity is likely to be reduced during darkness, which  
168 has been shown in other species of pinniped (Schusterman and Balliet 1971,  
169 Schusterman 1974). Therefore, it is highly likely that individuals are responding to  
170 olfactory and auditory, rather than visual cues at nighttime. In addition, the percentage  
171 of time pups spent active during nighttime decreased (which may also be attributed to  
172 visual acuity), and given that females respond to their pup's behavior (Fogdon 1971;  
173 Kovacs 1987; Smiseth and Lorentsen 1995*a, b*; 2001) this is also likely to reduce the  
174 need for maternal vigilance behavior at nighttime, and thus allow more time for rest.



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176           The findings presented here show that there is a significant difference in how  
177 females and pups partition aspects of their activity budgets between daytime and  
178 nighttime. As such, caution should be exercised when daytime activity budgets are  
179 used to represent nocturnal behavior or are used to draw general conclusions on the  
180 energetics, maternal investment or mating behavior of gray seals during the breeding  
181 season (*e.g.*, assuming uniformity across the circadian cycle). Although the sample  
182 size is small, given the highly significant results, the pattern appears evident; females  
183 and pups do spend more time resting during the nighttime. To investigate variation in  
184 circadian patterns of the more rarely recorded behaviors (in order to quantify energy  
185 budgets, maternal investment or mating patterns, for example) then more extensive  
186 data on individuals (including adult males) for their entire duration on the breeding  
187 colony would be required, and perhaps a different sampling regime (*e.g.*, *ad libitum* or  
188 focal sampling) depending on the behavior of interest (Altmann 1974).

189

190           This preliminary study has provided information that has been previously  
191 unavailable, adding to our knowledge of gray seal activity whilst on the breeding  
192 colony and provides a good example of what can be achieved with current,  
193 commercially available night-vision technology.

194

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343 *Table 1.* The names, abbreviations (in parentheses) and definitions of each of the nine behavioral categories, \* indicates the behavior is  
 344 applicable to females, ^ indicates the behavior is applicable to pups. The activity budget was based on the behavioral categories and definitions  
 345 presented in Anderson (1978), Anderson and Harwood (1985) and Kovacs (1987).

346

Behavior	Definition
Resting (R) *^	Non-active state lying with head on the ground, eyes may be open or closed.
Vigilance (VIG)*	Looking generally around or in the direction of an event, typically the head is up and neck extended. This includes a definite, distinct and directed look to their pup.
Comfort Move (CM)*	Makes adjustments to position and/or shuffles body on the spot but remains in the same geographical location. May also scratch themselves with their flippers.
Locomotion (L)*	Changes geographic location. This behavior may involve the use of the fore-flippers (for forward or backwards motion), 'barrel' rolling or shuffling (for sideways motion; note the distinction between shuffling on the spot (see 'Comfort Move'), and shuffling to change geographic location). This behavioral category excludes chasing behaviors (see 'Aggression').
Active (ACT)^	All active behaviors ( <i>i.e.</i> , when the pup is not 'Resting'), with the exceptions of 'Energy Transfer' and 'Social Interactions'.



Energy Transfer (ET)*^	The female lies on her flank exposing her nipples to the pup, at which point the pup will typically bring its nose to its mother's nipples. The mother is considered to be nursing when the pup makes oral contact with a nipple. This behavioral category represents time spent in behaviors that are associated with energy transfer to the pup.
Social Interactions (SINT)*^	The female physically interacts with her pup and/or vice versa, this includes (but is not limited to) nosing (touching the pup/mother with their nose) and flippering (using their flipper to 'stroke' their pup/mother). This behavioral category represents time spent in behaviors that are associated with social interactions between the mother and her pup.
Aggression (AGG)*	Includes but is not limited to; wailing (a vocal threat); aggressive flippering (the female vigorously 'waves' her flipper towards the perceived threat, and may make contact); slapping (the female will lie on her side and continuously slap her flipper against her flank); open mouth threats (the female will open her mouth baring her teeth at the perceived threat); lunging (the female extends her neck, lunging towards the perceived threat); biting (if the female makes contact they attempt to bite) and chasing (the female chases the perceived threat, this is the same as 'Locomotion' but with the clear intent of chasing the perceived threat).
Sex (SEX)*	A male mounts or attempts to mount the female. The male uses his jaws to grip the female by the neck and uses his fore-flippers to grip her body. Copulation attempts may be unsuccessful; this can occur if the female is unreceptive (typically

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resulting in aggressive behaviors on the female's part). A successful copulation occurs when intromission is clearly achieved and the copulation proceeded, uninterrupted, to completion.

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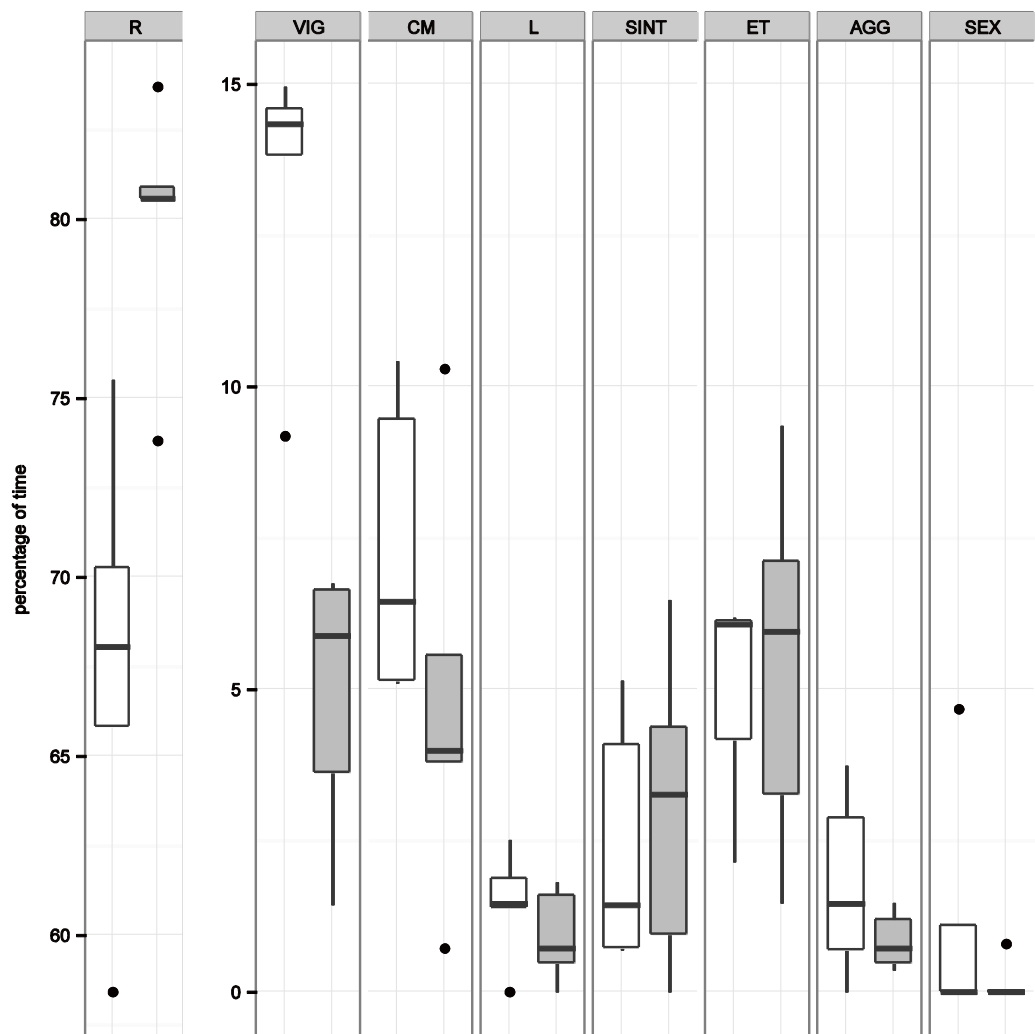
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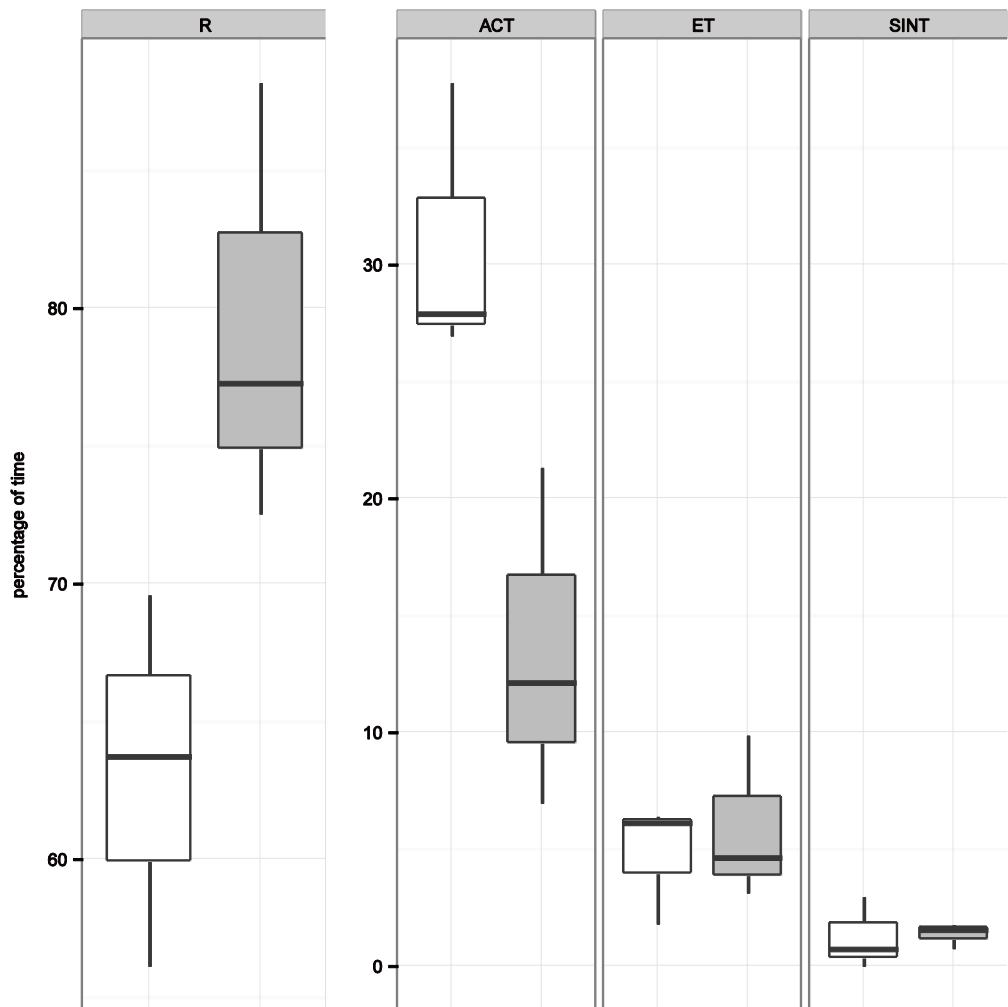
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362 *Figure 1.* The percentage of time females ( $n = 5$ ) spent in each of the eight behavioral  
363 categories (see Table 1 for definitions of behavioral categories) during daytime (white  
364 boxplots) and nighttime (gray boxplots) observations. ‘Resting’ (R) is presented in a  
365 separate plot, as it constitutes a considerably larger percentage of time spent than the  
366 other behavioral categories. The boxplots show the lower quartile, the median, the  
367 upper quartile and the whiskers, which extend to the most extreme data point that is  
368 no more than 1.5 times the inter-quartile range from the box.

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371

372 *Figure 2.* The percentage of time pups ( $n = 3$ ) spent in each of the four behavioral  
373 categories (see Table 1 for definitions of behavioral categories) during daytime (white  
374 boxplots) and nighttime (gray boxplots) observations. ‘Resting’ (R) is presented in a  
375 separate plot, as it constitutes a considerably larger percentage of time spent than the  
376 other behavioral categories. The boxplots show the lower quartile, the median, the  
377 upper quartile and the whiskers, which extend to the most extreme data point that is  
378 no more than 1.5 times the inter-quartile range from the box.